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Plant defence mechanisms: relevance to agriculture in Africa

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A vital priority for Africa today is to feed its burgeoning population while sustaining agricultural production and safeguarding the natural environment. It is anticipated that agricultural biotechnology will suit the African farming community excellently in terms of acceptability and affordability, and therefore make a major contribution towards the improvement of food production and alleviation of poverty. A major hurdle towards food production in Africa is the huge crop losses caused by pests and diseases. In addition to the fact that control by means of pesticides is often harmful to the environment, a great proportion of the African farmers, especially subsistence farmers, do not have access to modern pesticides. Inherent resistance provided via the seed, thus harnessing the plant's own defence mechanisms, would be one of the simplest solutions to pest and disease control in Africa. It boils down to the fact that plant biologists have to incorporate the technology into the seed. Otherwise, other methods of harnessing the plant's defence mechanisms have to be devised. Key events of the plant's defence mechanisms are discussed in relation to resistance manipulation. They include eliciting, with special reference to resistance (R) genes, and signalling events, the hypersensitive response (HR) and systemic acquired resistance (SAR). In this regard, recent insights and potential applications are accentuated. It is concluded that plant biologists have a major task to continue studies on plant defence mechanisms in an effort to provide fresh insights for the design of new and effective disease control strategies. The importance of such research in Africa, especially in the public sector, is stressed. Also, it is emphasised that the technological outcomes of the research should be protected in patents and made available to African farmers at affordable prices. Another challenge is the application of modern biotechnology in Africa; however, when packaged in the seed, the application of this cutting-edge concept would become natural, even to the most traditional farmer.

Introduction

Despite adverse reaction to genetically modified (GM) crops, the application of biotechnology in agriculture is increasing rapidly in First World countries. Already it is said that the agricultural biotechnology revolution is also occurring in developed countries. Between 1996 and 1998, the global area of transgenic crops increased 15-fold. In 1998, the USA contributed 74% of the transgenic crop area (Ives and Wambugu 1999). The estimated global area of transgenic crops for 2001 was 52.6 million ha. An equivalent of 13.5 million ha was grown in six developing countries (James 2001). Although needing to improve food production, Africa lags far behind in the use of agricultural biotechnology.

The African economy on average is 70% based on agriculture. Agriculture employs 50–75% of the labour force yet Africa still imports 25% of its grain requirements. The continent's crop production per unit area of land is the lowest in the world; the average maize yield is about 1.7 tonnes ha^{-1} compared to a global average of 4 tonnes ha^{-1}. The population in Africa is expected to double in the next 25 years, which calls for urgent improvement of food production (Ives and Wambugu 1999, Wambugu 1999, M'Poko 2001). Any effort to improve crop production should take into account the subsistence way of farming on smallholdings by mostly poor and untrained farmers. One of the challenges would be to increase small-holder agriculture productivity by producing more on less land, while maintaining or enhancing the quality of the environment and conserving natural resources. To achieve these goals, harnessing of agricultural biotechnology is an important avenue. Increasingly, plant biotechnology is considered as an important tool in creating an eco-efficient environment where more food can be produced while simultaneously minimising the impact of agriculture and resource use on the environment. A Harvest Chief Executive Officer, Dr Florence Wambugu, has said 'Never has Africa needed sustainable solutions to poverty, hunger and malnutrition like today. We must think outside the box when it comes to increasing smallholder agriculture productivity and promoting food security' (Monsanto Africa 2003).

African agriculture suffers from huge crop losses as a result of pre- and post-harvest pest and disease damage.

(United Nations Report 2001). Beyond doubt, effective pest and disease control will enhance agricultural productivity in Africa. Control of virus diseases alone has the potential to double the African production. Maize streak virus (MSV) causes losses of 100% of the crop in many parts of Kenya and other African countries (Ives and Wambugu 1999). At present, methods of pest and disease control generally involve spraying of pesticides, mostly several times during the growing season. Chemicals used to control pests and diseases of plants are usually expensive. Application of these chemicals can be complicated, often highly technological and costly. In addition, they can be harmful to the environment because of toxicity to other organisms and pollution of drinking water. In cases of insufficient precautionary measures it might even affect the health of humans handling it or in one way or another come into contact with it. The lethality of pesticides to harmless organisms often contribute to resurgence of pest populations and the creation of secondary pests (Chrispeels and Sadava 1994).

Agricultural biotechnology, whereby seeds are improved or simple, safe control methods are developed to provide resistance to insects and diseases, holds great promise for Africa where poverty, lack of appropriate training and sometimes poor growing conditions make farming difficult. Pesticides, machinery, fuel and other modern equipment which are routinely used by farmers of rich countries are luxuries for probably the largest proportion of African farmers.

Most pesticides are developed to kill invading organisms directly. Alternatively, the plant's own defence mechanisms can be harnessed to control pests and diseases. Resistance provided via seed is one of the simplest solutions to pest and disease control. In addition, genetic resistance is the most cost effective and environmentally safe solutions (Agrios 1988, Cornelissen and Melchers 1993). The introduction of pest and pathogen resistance genes into crop plants was first exclusively done by breeding and currently it is also possible through genetic engineering.

A number of plant disease resistance genes (R-genes) used in resistance breeding programmes for decades have been clearly defined by conventional genetics (Flor 1971, Agrios 1988). Although much effort has been invested in understanding innate resistance mechanisms in plants, our knowledge of how these genes function and how plants resist pathogens is still fragmentary. The evolution of new variants of most pathogens and new resistant-breaking biotypes of insects necessitates a corresponding increase in our understanding of resistance and our ability to utilise it. Also, to exploit biotechnological strategies for controlling pests and diseases of plants a more comprehensive understanding of the mechanisms that underlie resistance responses is needed.

Actually, in plants, resistance is the rule and susceptibility the exception. Although plants are constantly exposed to parasitic organisms, disease seldom develops (Bell 1980, Lamb *et al.* 1992). The plant has many defence mechanisms that can result in resistance. So-called passive defence is due to physical and chemical preformed or constitutive factors. This includes physical barriers such as the cell wall and cuticle, as well as chemical defence often due to phenolics, alkaloids and proteins. The active defence mechanism is induced when the invader is perceived by the plant. Perception is caused by elicitors, deriving from the pathogen or plant (damage/stress) binding to receptors in the membranes. This leads to the production of signalling compounds that activate the expression of genes encountered in the defence response (Johal *et al*. 1995).

A very effective arsenal of inducible defence responses can be activated. This includes the hypersensitive response (HR), a cell-death programme of infected and neighbouring cells, as well as tissue reinforcement and antibiotic production at the site of infection (Hammond-Kosack and Jones 1996). The local responses can consequently trigger a long-lasting systemic response (Systemic Acquired Resistance, SAR) that conditions the plant for resistance against a broad spectrum of pathogens. Evidence suggests that SAR-signalling is mediated, directly or indirectly, by salicylic acid (SA) produced during the HR (Dong 2001, Métraux 2001). The HR during basic incompatibility (general resistance) can be induced non-specifically by a variety of substances of both biotic and abiotic origin (general elicitors). The HR can also be induced specifically by the interaction of products encoded by resistance (R) genes of the host and avirulence (Avr) genes of the pathogen that correspond in a gene-for-gene fashion. The latter type of resistance is referred to as host incompatibility or specific resistance (Johal *et al.* 1995).

For decades R genes appealed to plant breeders because in many cases a single R gene, when bred into a susceptible plant of the same species, can provide complete resistance to one or more strains of a particular pathogen. The introduction of R genes into crop cultivars by conventional breeding is a lengthy process and they are often quickly defeated by pathogens (Pink 2002). Moreover, many R genes do not provide broad-spectrum resistance. Advances in our basic understanding of R gene-dependent resistance might provide strategies to overcome these deficiencies in future (McDowell and Woffenden 2003). Quite a number of R genes, against many different pathogens, have now been cloned from a variety of plants, which allows the investigation of their molecular modes of action as well as identifying resistance gene analogues by sequence similarities. More directed and faster creation of resistant cultivars by transformation of elite cultivars with these cloned characterised R genes is becoming feasible (McDowell and Woffenden 2003). Marker-assisted breeding will also contribute to more efficient development of new resistant varieties. In this regard for example, genes closely tied to SAR could be useful for marker-assisted breeding of varieties with improved potential for SAR (Sticher *et al.* 1997).

Investigations of non-host resistance (basic incompatibility) might reveal useful genes for better durability and perhaps novel tools for engineering resistance (McDowell and Woffenden 2003).

Many R genes have a narrow range of resistance. In genetic, biochemical and physiological studies on plant defence mechanisms a variety of defence signals have been identified (Feys and Parker 2000, McDowell and Dangl 2000). In principle, each signalling component is a putative switch for activating the defence arsenal. Significant advances in the understanding of signal transduction pathways that mediate the resistance response could lead to the next generation of transgenic plants in which manipulation of key signalling components results in the activation of a broad array of host defences. In addition to broad spectrum resistance, this approach is likely to deliver durable resistance. Alternatively, the signalling pathway might be altered so that it is primed more rapidly and effectively to activate these defence arsenals upon infection.

An alternative approach to the transgenic ones is to enhance resistance through treatment with compounds that activate part or all of the host defence arsenals (McDowell and Woffenden 2003). Available evidence suggests that in the plant systemic acquired resistance (SAR) signalling is mediated, directly or indirectly by salicylic acid (SA) (Chen *et al.* 1993). In consequence hereof, SA and aspirin (acetyl salicylate) have been identified as plant defence activators. Also, 2,6-dichloroisonicotinic acid (INA) and benzothiadiazole (BTH) appear to be functional analogs of SA. BTH is being used commercially as a plant protecting agent. Other chemical activators of SAR, both natural and synthetic substances, have been identified (Sticher *et al.* 1997). Oxygenated lipids and oligomers of chitosan are outstanding candidates in this regard. Hydroxylated fatty acids can act as antimicrobial compounds and endogenous elicitors (Kessman *et al.* 1994).

Although plant defence activators still have to be applied, e.g. as a foliar spray, their use poses a more environmentally friendly approach than the use of pesticides to control plant diseases and pests. They have the advantage of not being toxic to organisms in the environment. For use in developing countries uncomplicated application methods are preferred, e.g. as a seed dressing.

Another genetic modification strategy has concentrated on the debilitation of the pathogen. A range of PR (pathogenesis-related) proteins are expressed during the HR (Fritig *et al*. 1998). Beta-1,3-glucanase and chitinase are two PR-proteins with hydrolytic enzyme activity and are able to digest microbial cell walls. Their and other PR-protein genes have been used with varying degrees of success in plant transformation experiments (Kessman *et al.* 1994). It is now anticipated that by using DNA shuffling techniques variant chitinases, with 30–50-fold enhanced activity, can be deployed in combination with antimicrobial proteins to produce resistance in transgenic plants (Hammond-Kosack and Parker 2003).

Semiochemicals have been proposed as tools in the development of plant protection strategies against insects (Chamberlain *et al.* 2000, Ninkovic *et al.* 2003). These compounds may attract parasitoids or predators of insects or repel insects. Among such semiochemicals are plant stress signals associated with the induction of defence systems. Plant manipulation which allow appropriate semiochemicals to be generated when plants are attacked is envisaged (Chamberlain *et al*. 2000).

From a somewhat different perspective, genes from other organisms have been used with great success in plant transformation. For example, transgenic plants containing the Bt-gene from the bacterium, *Bacillus thuringiensis,* are widely used to control epidopteran insects in crops (Chrispeels and Sadava 1994). In this regard, the use of Bt cotton by some smallholder farmers in one of the cotton areas of South Africa has been a great success (Ismael *et al.* 2001).

From the preceding paragraphs it is clear that many useful, mostly putative, applications are already being developed or envisaged from our relatively limited knowledge base on plant defence mechanisms and others will undoubtedly follow as our level of basic understanding grows. For example, our understanding especially of eliciting events and the signal transduction network is still fragmentary. It is anticipated that continuous research will provide fresh insights in the design of new and effective disease control strategies. A major task for plant biologists is to identify useful genes and devise clever schemes for their deployment.

In first world countries, investment in agricultural biotechnology has been dominated by the private sector. It seems that much of this ‘private’ research is concentrated on problem solving that can be marketed primarily in the rich industrial nations, since these countries have the buying power to bring the return on investments aimed for. Although special agreements with regard to developing countries, particularly in Africa, can be envisaged it is unrealistic to expect private enterprise to disregard market-oriented pricing of technology for charitable reasons (Ives and Wambugu 1999). On the other hand, African agriculture has its own unique predicaments, which can be attended to best under local conditions. For these reasons public research in Africa is called for. The technological outcomes of the research should be protected in patents and made available at affordable prices to local farmers. Although a number of countries in Africa do have impressive national biotechnology research programmes, many more investments in this regard are needed (Ives and Wambugu 1999).

Another challenge in Africa would be to put modern biotechnology to use, especially amongst small-scale, resource-poor farmers who form the large proportion of the farming community. However, the advantages of technology especially when ‘packaged in the seed’ is that traditional farmers know how to use it and that its use has minimal impact on local cultural practices.

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